3

Bryozoa : The Miocene to Recent family Petalostegidae. Systematics, affinities, biogeography

Dennis P. GORDON

New Zealand Oceanographic Institute
DSIR Marine and Freshwater
Private Bag, Kilbirnie
Wellington, New Zealand

&

Jean-Loup d'HONDT

Muséum national d'Histoire naturelle
Laboratoire de Biologie des Invertébrés marins et Malacologie
57, rue Cuvier
75005 Paris, France

ABSTRACT

Knowledge of the little-known cheilostome bryozoan family Petalostegidae has hitherto been based on only two extant species (*Petalostegus bicornis* (Busk) and *P. spinosus* Powell), and an Australian Miocene species (*P. tenuis* (Maplestone)). Previously, these have been included among the anascan superfamily Buguloidea. With the discovery of a remarkably diverse petalostegid fauna in New Caledonian waters (especially on the northern Norfolk Ridge), it is apparent that the family is neither " anascan " nor monogeneric. The obscure monotypic Australian Miocene genus *Chelidozoum* Stach is now recognised as petalostegid, based on the discovery of four, new, Recent species (including one from off Victoria). Among these species there is a reduction in the size of the costal field from five spines, through three, to two. The known species of *Petalostegus* Levinsen are redescribed and four new species are described (including one from the New Zealand deep sea). The family, which is entirely southern-hemisphere in distribution, is now included in the ascophorine superfamily Catenicelloidea.

Evidence of predation on embryos is seen from boreholes in ovicells of two species of *Petalostegus*.

GORDON, D.P. & d'HONDT, J.-L., 1991. — Bryozoa : The Miocene to Recent family Petalostegidae. Systematics, affinities, biogeography. *In* : A. CROSNIER (ed.), Résultats des Campagnes MUSORSTOM, Volume 8. *Mém. Mus. natn. Hist. nat.*, (A), **151** : 91-123. Paris ISBN : 2-85653-186-5.

Publié le 8 novembre 1991.

RÉSUMÉ

Bryozoa : La famille des Petalostegidae (du Miocène à l'Actuel). Systématique, affinités, biogéographie.

Les connaissances actuelles sur une famille de Bryozoaires Cheilostomes peu connue, celle des Petalostegidae, n'étaient jusqu'à présent fondées que sur deux espèces récentes, *Petalostegus bicornis* (Busk) et *P. spinosus* (Powell), et une espèce fossile australiennne connue des terrains miocènes, *P. tenuis* (Maplestone). Elles étaient jusqu'à présent incluses dans la superfamille des Buguloidea, classée parmi les Anascina. Par suite de la découverte d'une riche diversité spécifique de Petalostegidae dans les eaux de Nouvelle-Calédonie (et tout particulièrement dans la région septentrionale de la ride de Norfolk), il est apparu que cette famille n'était ni monogénérique ni à classer parmi les Anascina. Le genre *Chelidozoum* Stach, considéré comme monotypique et exclusivement connu du Miocène australien, est maintenant rangé dans la famille Petalostegidae, consécutivement à la découverte et l'étude de quatre espèces nouvelles actuelles, dont l'une récoltée au large de Victoria (*C. quinarium* sp. nov., *C. ternarium* sp. nov., *C. binarium* sp. nov. et *C. pararium* sp. nov.). Ce groupe d'espèces se caractérise par la réduction progressive du bouclier costal frontal, qui se manifeste par la diminution du nombre d'épines modifiées coalescentes qui le constituent ; ce nombre passe de cinq à trois et deux. Les espèces du genre *Petalostegus* Levinsen, précédemment connues, sont ici redécrites ; quatre nouvelles espèces (dont l'une originaire des grands fonds au large de la Nouvelle-Zélande) sont décrites dans ce travail : *P. scopulus* sp. nov., *P. trimorphus* sp. nov ; *P. harmeri* sp. nov. et *P. vexillum* sp. nov. La distribution géographique de cette famille est limitée à l'hémisphère sud. Sa répartition bathymétrique et stratigraphique est récapitulée. Les présentes recherches permettent d'inclure la famille Petalostegidae parmi les Ascophorina, et de la ranger, à présent, dans la superfamille Catenicelloidea. Certains des ovicelles observées présentent des traces de prédation imputables à des Mollusques.

INTRODUCTION

The cheilostome family Petalostegidae was established by GORDON (1984) for the genus *Petalostegus* Levinsen, 1909. *Petalostegus*, with type species *Catenaria bicornis* Busk, 1884, is a genus of delicate, branching uniserial colonies in which the claviform zooids have a shield of five more-or-less petaloid spines protecting the underlying membranous frontal wall. LEVINSEN (1909) included the genus in his heterogeneous new family Bicellariellidae along with *Bugula*, *Beania*, *Chaperia*, *Hiantopora*, and others, and in this he was followed by CANU & BASSLER (1927, 1929), BASSLER (1953), and LARWOOD (1969), but any supposed affinities with the buguloidean bryozoans is entirely superficial, based on the erect branching and delicate construction. On the other hand, HARMER (1957) remarked on the similarity of *Petalostegus* to the Alysidiidae. This family (especially *Catenicula*) has in common a similar colonial morphology, with spine-like kenozooids arising from terminal and subterminal zooids. *Petalostegus*, however, lacks the cryptocyst of alysidiids [HARMER (1957) interpreted it as " suppressed "], has a shield of spines, and a different ovicellular arrangement. POWELL (1967) and HAYWARD & COOK (1979) also included *Petalostegus* in the Alysidiidae. GORDON (1984) compared the petaloid spines of the frontal shield to the scutal spines in *Caberea* and, while recognising the need for a separate family Petalostegidae, included it in the superfamily Buguloidea near the Cabereidae.

The recent cruises of ORSTOM and the Muséum national d'Histoire naturelle in New Caledonian waters have yielded remarkable new data about the family Petalostegidae which allow a definitive statement on the systematic relationships and biogeography of this family. In particular, the diversity of *Petalostegus* species in such a limited area is surprising and especially noteworthy is the discovery of several new species of *Chelidozoum* Stach, a hitherto monotypic Australian genus not previously recognised as petalostegid, and known only from the Miocene.

This material has provided an opportunity to review the family, describing or redescribing all known species, and commenting on their systematic relationships and biogeography.

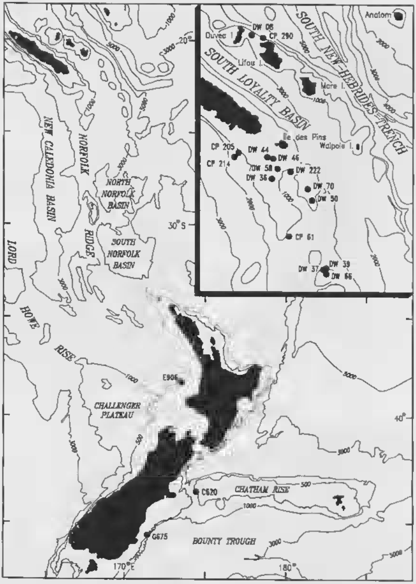


FIG. 1. — Map showing New Caledonian and New Zealand station locations mentioned in the text. Depths are in metres.

LIST OF STATIONS

The locations of the stations listed below are shown in figure 1.

New Caledonia

BIOCAL

Station DW 08. — 12.08.1985, 20°34.35′ S, 166°53.90′ E, 435 m : *Chelidozoum quinarium.*

Station DW 36. — 29.08.1985, 23°08.64′ S, 167°10.99′ E, 650 m : *Chelidozoum ternarium, Petalostegus harmeri.*

Station DW 44. — 30.08.1985, 22°47.30′ S, 167°14.30′ E, 440 m : *Chelidozoum ternarium.*

Station DW 46. — 30.08.1985, 22°53.05′ S, 167°17.08′ E, 570 m : *Chelidozoum quinarium, C. ternarium, Petalostegus bicornis, P. harmeri, P. vexillum.*

Station CP 61. — 02.09.1985, 24°11.67′ S, 167°31.37′ E, 1070 m : *Petalostegus bicornis.*

Station DW 66. — 03.09.1985, 24°55.43′ S, 168°21.67′ E, 515 m : *Chelidozoum quinarium, Petalostegus harmeri, P. scopulus, P. spinosus.*

Station DW 70. — 04.09.1985, 23°24.70′ S, 167°53.65′ E, 965 m : *Petalostegus scopulus.*

MUSORSTOM 4

Station DW 222. — 30.09.1985, 22°57.60′ S, 167°33.00′ E, 410-440 m : *Chelidozoum ternarium.*

BIOGEOCAL

Station CP 205. — 08.08.1987, 22°40.61′ S, 166°28.01′ E, 1350-1380 m : *Petalostegus bicornis.*

Station CP 214. — 09.04.1987, 22°43.09′ S, 166°27.19′ E, 1665-1590 m : *Petalostegus bicornis.*

Station CP 290. — 27.04.1987, 20°36.91′ S, 167°03.34′ E, 920-760 m : *Petalostegus bicornis.*

SMIB 4

Station DW 37. — 07.03.1989, 24°54.5′ S, 168°22.3′ E, 540 m : *Petalostegus harmeri.*

Station DW 39. – 07.03.1989, 24°56.2′ S, 168°21,5′ E, 560 m : *Petalostegus harmeri, P. spinosus.*

Station DW 50. — 09.03.1989, 23°42.2′ S, 168°00.8′ E, 295 m : *Chelidozoum binarium.*

Station DW 58. — 09.03.1989, 22°59.8′ S, 167°24.2′ E, 560 m : *Petalostegus vexillum.*

New Zealand

New Zealand Oceanographic Institute

Station C620. — 02.05.1961, 43°40′ S, 174°47′ W, 752-737 m : *Petalostegus trimorphus.*

Station E906. — 28.03.1968, 38°39′ S, 172°38′ E, 691-751 m : *Petalostegus trimorphus.*

Station G675. — 19.01.1970, 45°27′ S, 171°24′ E, 792 m : *Petalostegus trimorphus.*

SYSTEMATIC ACCOUNT

Suborder ASCOPHORINA Levinsen, 1909

Infraorder CRIBRIOMORPHA Harmer, 1926

Superfamily CATENICELLOIDEA Busk, 1852

Family PETALOSTEGIDAE Gordon, 1984

DIAGNOSIS. — Colony erect, uniserial and branching, delicate, anchored by rhizoids. Main axes kenozooidal or autozooidal. Kenozooids elongate-claviform with small subterminal opesia or spine-like. Autozooids with dilatation and cauda, the frontal shield a gymnocyst with a variable field of 2-5 flattened costal spines including the pair that define the proximal rim of the orifice. Avicularia adventitious, mostly present on autozooids, occasionally on kenozooids. Fertile zooid mostly different from autozooid, with ovicell as large as or larger than the maternal dilatation ; costal field present.

RANGE. — Langhian (Lower Miocene) to Recent.

Genus *PETALOSTEGUS* Levinsen, 1909

DIAGNOSIS. — Main axes of colony composed of autozooids, kenozooids borne on terminal or subterminal autozooids. Autozooids with a large costal field of five petaloid spines, the gymnocyst reduced, the dilatation not markedly bent forward. Orifice more or less semicircular. Avicularia sessile, at the distolateral corners of each autozooid, or one or both of these replaced by spine-like avicularia or kenozooids ; short claviform avicularia occasionally produced from claviform kenozooids with opesiae. Fertile zooid with five or six costal spines, the ovicell large, typically with median suture and distal foramen. Rhizoids issue from small holes just proximal to the costal field in autozooids.

RANGE. — Langhian (Lower Miocene) to Recent.

TYPE SPECIES. — *Catenaria bicornis* Busk, 1884.

Petalostegus bicornis (Busk, 1884)

Fig. 2. Pls 1, A-F ; 8, A

Catenaria bicornis Busk, 1884 : 14, pl. 2, fig. 2. — WATERS, 1889 : 9, pl. 1, fig. 1. — JELLY, 1889 : 34.
Petalostegus bicornis - LEVINSEN, 1909 : 114, pl. 9, fig. 8. — CANU & BASSLER, 1929 : 232, figs 89, 94. — BASSLER, 1953 : G181, fig. 138.4. — HARMER, 1957 : 642 part, fig. 118, pl. 51, fig. 15. — LARWOOD, 1969 : 175, fig. 2. — ? HAYWARD & COOK, 1979 : 68. — ? GORDON, 1986 : 59.

TYPE MATERIAL. — Holotype, The Natural History Museum, London, slide 87.12.9.46.

TYPE LOCALITY. — " *Challenger* " Stn 280, 18°40′ S, 149°52′ W, near Tahiti, 3548 m, on *Globigerina* ooze.

MATERIAL EXAMINED. — **Polynesia.** The Natural History Museum : Holotype slide 87.12.9.46.
New Caledonia. BIOCAL : stn DW 46, 570 m. — Stn CP 61, 1070 m.
BIOGEOCAL : stn CP 205, 1350-1380 m. — Stn CP 214, 1665-1590 m. — Stn CP 290, 920-760 m.

DESCRIPTION OF HOLOTYPE. — Colony fragments (2) about 12.5 mm long, comprising straight axial chains of autozooids each of which produces, from a geniculate swelling of the autozooidal dilatation, alternately to left and right up the axis, a " secondary " once- or twice-dichotomous branch of autozooids. [These branches are actually tertiary, but the true primary axis is lacking from the holotype.] Autozooids 0.72-1.13 mm total length, the cauda ranging from 0.32 mm to 0.68 mm in length and the dilatation 0.40-0.45 x 0.23-0.28 mm, the costal shield rather inflated, comprising 5 costae, of which the midproximal one is largest and the midlateral one on the nongeniculate side of the

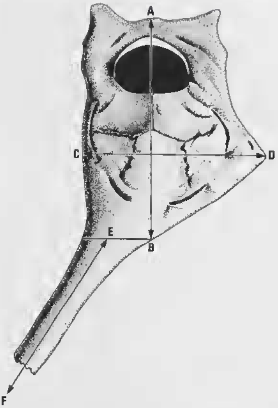


FIG. 2. — Drawing of the zooid of *Petalostegus bicornis* shown in Plate 1, A, showing the axes from which measurements were taken for all

Petalostegus autozooids, viz. A-B (length of dilatation) ; C-D (width of dilatation) ; E-F (length of cauda).

zooid typically smallest ; generally 2-3 sutural pores between the three proximal costae and 1-2 between the suboral ones or these latter pores much reduced. Geniculation (knee-like protuberance of one side) adjacent to mid- or distal part of costal shield. Orifice 0.106-0.119 mm wide and 0.069 mm high. Avicularia elongate, the palatal surface often nearly parallel to the nongeniculate side of the dilatation, facing nearly directly lateral or, more usually, slightly backward. Kenozooids present as long (up to 1.26 mm) spines arising from the middistal budding site of the terminal zooids of secondary branches and from the geniculate process of penultimate zooids. Fertile segment large, borne on the geniculate process of the penultimate zooid of a " secondary " branch ; ovicell longer (0.47 mm) and wider

(0.41 mm) than maternal zooid (0.35 mm long, 0.38 mm wide) and 0.43 mm deep, the cauda 0.25 mm long, at an angle of about 135° relative to the longitudinal axis of the zooid ; maternal zooid with 6 costae in the shield, the largest costa nearest the cauda, the suboral pair each with a stout median carina so that this pair is rather shelf-like ; geniculate process lacking a pore ; ovicell with a thin median longitudinal suture and 2 umbones - in front and back with a large foramen in front of the latter ; avicularia of fertile zooid adjacent to orifice, somewhat projecting, the palatal surface facing laterally on one side, slightly behind on the other.

DISTRIBUTION. — Near Tahiti, 3548 m ; southwestern New Zealand, 463-1003 m ; New Caledonia and northern Norfolk Ridge, 570-1590 m ; ? eastern South Africa, 1000-1200 m.

REMARKS. — The New Caledonian material must be discussed in relation to the holotype for there are some differences and additional features.

The primary axis of the largest specimen in the collection is 55 mm long. The autozooids making up this axis and the axes of the secondary branches have long caudae. At the top of each cauda on the geniculate side near the costal field is a rhizoid foramen. The rhizoids collectively descend the main axis of inactive autozooids and spread out basally to anchor onto foraminiferan grains.

The greater range of zooidal dimensions exhibited by the New Caledonian material mostly includes those of the holotype, but the dilatation length is slightly greater in some holotype zooids. The most significant difference is in the fertile segment. While resembling that of the holotype in overall shape, those in the ORSTOM material are somewhat smaller, narrower, and with a very short cauda. Importantly, however, the costal field comprises six spines (one sometimes vestigial) and the suboral pair can be carinate. For this reason we conclude that the ORSTOM specimens are conspecific with *Petalostegus bicornis.*

It is clear from the range of material in the ORSTOM collections that some previous records of *Petalostegus* were wrongly attributed to *P. bicornis* ; for example, apart from the ovicell of the holotype specimen and the stylised figure of an autozooid, the illustrations in HARMER (1957) are not of *P. bicornis* but of *P. harmeri* n. sp. Similarly, the record of *P. bicornis* from the Kermadec Ridge (GORDON, 1984) is of a yet undescribed species. It has larger intercostal lacunae and autozooids may be produced from opesiulate kenozooids, which is not the case in *P. bicornis.* Without information on fertile zooids the identity of HAYWARD and COOK's (1977) record of *P. bicornis* from South Africa remains uncertain. Where possible, it is highly desirable to illustrate the distinctive fertile segment because the range of autozooidal characters can overlap somewhat among the species.

HASTINGS's and HARMER's illustrations of the holotype ovicell of *P. bicornis* (in HARMER, 1957 : fig. 118, and plate 51, fig. 15, respectively) fail to show the six elements of the costal shield of the maternal zooid although these are clearly seen in the holotype specimen. Six is not the usual number in *Petalostegus* and is found only in *P. scopulus* sp. nov. among the other species of the genus. The so-called " calcareous shelf or plate " (HARMER, 1957 : 644) inside the orifice of the holotype ovicell is not present in cleaned, scanned ORSTOM specimens and appears to be some dried tissue.

Petalostegus scopulus sp. nov.

Pl. 2, G-L

MATERIAL EXAMINED. — **New Caledonia.** BIOCAL : stn DW 66, 515 m. — Stn DW 70, 965 m.

DESCRIPTION. — Colony to 37 mm high, more or less like that of *P. bicornis*, with an axis of long-caudate autozooids giving rise to secondary (then tertiary and quaternary) branches alternately to left and right up the stem. Autozooids 0.51-0.90 mm total length, the cauda ranging from 0.14 mm to 0.56 mm in length and the dilatation 0.32-0.34 x 0.24-0.26 mm, the costal shield somewhat inflated, comprising 5 costae, the 3 proximal ones about the same size ; generally 3-4 small sutural pores between the suboral costae and 5-6 between the other costae. Geniculation adjacent to the mid-part of the costal shield. Orifice 0.064-0.085 mm wide and 0.042-0.058 mm high. Avicularia always paired, more or less identical to those of *P. bicornis* but with variable orientation - both face either laterally (not slightly backwards), or frontally, or only one may face frontally, and one may even be lacking (but this is not common). Branches terminate in regular-sized autozooids with spine-like kenozooids (up to 1.07 mm long) or reduced zooids with 3-4 costae and vestigial orifice - these often have 3 kenozooidal spines and a small avicularium or 2 spines and 2 small avicularia. Fertile segment not especially large, borne from the geniculation of an autozooid in a tertiary or quaternary branch ; ovicell longer (0.54 mm) and narrower (0.22 mm) than maternal zooid (0.26 x 0.30 mm) and 0.30 mm deep, the cauda 0.15 mm long, at an angle of about 112° relative to the longitudinal axis of the zooid ; maternal zooid with 6 costae in the shield, the midlateral ones smallest ; geniculate process lacking a pore ; ovicell with an anterodistal proboscis-like prolongation creased by a median suture and uncalcified apically ; adjacent to a much smaller dorsal umbo is a relatively large foramen ; avicularia of fertile zooid facing frontally.

Types. — *Holotype* : Colony from Biocal Stn DW 70, 23°24.70′ S, 167°53.65′ E, 965 m, northern Norfolk Ridge (MNHN-Bry-16636). No paratypes.

Distribution. — Northern Norfolk Ridge, 515-965 m.

Remarks. — In the absence of ovicells, *Petalostegus scopulus* may be distinguished from *P. bicornis* by the inconsistent orientation of the autozooidal avicularia, and the presence of reduced autozooids, with fewer costae, in the distal ends of branches.

Like *P. bicornis*, the female zooids of *P. scopulus* have six spines comprising the costal shield.

The species name is a masculine Latin noun in apposition meaning projection, referring to the long prolongation of the ovicell.

Petalostegus trimorphus sp. nov.

Pl. 2, A-E

Material examined. — **New Zealand**. N.Z. Oceanographic Institute : stn C620, 752-737 m. — Stn E906, 691-751 m. — Stn G675, 792 m.

Description. — Colony to 46 mm high, delicate with long slender branches ; no main stem throughout and not every zooid produces a bifurcation. Autozooids long-caudate except in terminal branches, 0.74-3.93 mm in total length, the dilatation elongate, 0.47-0.56 x 0.23-0.34 mm, the costal shield somewhat inflated, comprising 5 costae, the midproximal one the largest ; generally a tiny sutural slit between the suboral costae and 2 such openings between the other costae. Geniculation adjacent to the distal flank of a lateral costa. Orifice high-arched, about as high as wide (0.092-1.11 mm). Avicularia always paired, with variable orientation, generally with the palatal surface facing distally or the avicularia more prominent, swollen-based and projecting, facing obliquely frontally. Branches terminate in autozooids whose sessile avicularia are replaced by long (up to 1.26 mm) spine-like avicularia or kenozooids, between which is another such polymorph from the distal budding site. Fertile segment large, ovicell 0.51 mm long, 0.36 mm wide, and 0.47 mm deep, with a tiny pair of frontal pores associated with the median suture ; a foramen occurs in front of the dorsal projection ; maternal zooid 0.58 x 0.36 mm, with 5 costae in the shield arranged as in autozooids but with larger intercostal foramina ; no geniculate process ; avicularia face more or less distally.

Types. — *Holotype* : Parts of a colony from NZOI Stn G675, 45°27′ S, 171°24′ E, 792 m, off Otago Shelf near head of Bounty Trough, NZOI H-599.

Paratypes : from NZOI Stn C620, 43°40′ S, 174°47′W, 752-737 m, NZOI, P-999 ; from NZOI Stn E906, 38°39′S, 172°38′E, 691-751 m, MNHN-Bry-18953.

Distribution. — Southeastern New Zealand (Chatham Islands slope ; head of Bounty Trough), and continental slope west of Taranaki, North Island, 691-792 m.

Remarks. — *Petalostegus trimorphus* is perhaps the most distinctive of all the Recent species, with the largest and longest zooids, open branching with no tendency to inward curling, and the bilaterally symmetrical fertile segments lacking a geniculation.

The species is named for the three forms of avicularia, highlighting another unique feature in the genus, viz. the long, tubiform avicularia resembling those of the bugulid genus *Cornucopina*.

Petalostegus harmeri sp. nov.

Pl. 3, A-G

Petalostegus bicornis (part) - HARMER, 1957 : 642, pl. 51, figs 13, 14, 16, 18.

MATERIAL EXAMINED. — **New Caledonia**. BIOCAL : stn DW 36, 650 m. — Stn DW 46, 570 m. — Stn DW 66, 515 m.

SMIB 4 : stn DW 37, 540 m. — Stn DW 39, 560 m.

DESCRIPTION. — Colony to 52 mm high, bushy, profusely branching, the pattern of branching more or less as in *P. scopulus*. Autozooids 0.53-1.11 mm total length, the cauda ranging from 0.24 mm to 0.71 mm in length and the dilatation 0.28-0.41 x 0.21-0.30 mm, somewhat bent forward in all but the primary branches. Costal shield somewhat inflated, the 3 proximal spines each generally larger than those of the suboral pair ; intercostal lacunae relatively large, generally 2 between the suboral pair of costae, 3-4 along the other sutures. Geniculation generally in the proximal half of the dilatation adjacent to the origin of a lateral costa or just distal to it. Orifice high-arched, 0.074-0.090 mm wide and 0.060-0.090 mm high. Avicularia paired, facing laterally or distolaterally or, more usually, one or both replaced by a cornute projection. Branches terminate in autozooids which produce, from their geniculations, kenozooids with a much-reduced round opesia, no costae, and either 4 long (up to 1.39 mm) spines of varying length or some lacking or one of the distolateral spines replaced by a small avicularium and/or another such kenozooid arises from the geniculation of the parent kenozooid. Fertile segment larger than autozooid, borne on a geniculation in a tertiary or quaternary branch ; ovicell about as long as dilatation but with spine-like prolongations that increase in overall length to about 0.45 mm, 0.24 mm wide and 0.36 mm deep ; maternal zooid 0.21-0.28 mm long and 0.28 mm wide, the cauda 0.21-0.30 mm long, curving somewhat obliquely at an angle of about 146° relative to the longitudinal axis of the zooid ; maternal zooid typically with 5 costae in the shield, with occasionally a vestigial 6th one, with conspicuous lacunae between the costae ; geniculate process on the distal half of the dilatation, always bearing a kenozooid with small opesia and distal spines ; ovicell with distal spine-like projections frontally and dorsally, the former with a median suture and slightly expanded distally ; a large foramen in front of the dorsal spine ; avicularia shortly subtubular, facing laterally.

TYPES. — *Holotype* : colony from BIOCAL Stn DW 66, 24°55.43′ S, 168°21.67′ E, 515 m, northern Norfolk Ridge, MNHN-Bry-18955.

Paratypes : MNHN-Bry 19956, and MNHN-Bry 16929, both from the same locality as the holotype ; MNHN-Bry 16637, from SMIB 4 Stn DW 37, 24°54.5′ S, 168°22.3′ E, 540 m ; MNHN-Bry 16631, from SMIB 4 Stn DW 39, 24°56.2 ′ S, 168°21.5′ E, 560 m ; NZOI, P-998, from same locality as holotype.

DISTRIBUTION. — Northern Norfolk Ridge, 515-650 m ; Indonesia : western Halmahera, Molucca Islands, 827 m.

REMARKS. — *Petalostegus harmeri* was illustrated by HARMER (1957) (as *P. bicornis*) from a "*Siboga*" station in the Moluccas (Indonesia). The species is readily distinguished from *P. bicornis* (and from all other species of *Petalostegus*) by the spine-like prolongations of the distolateral corners of autozooids, and the fact that the female zooid produces a kenozooidal branch from its geniculation. The illustration of the dorsal view of the ovicell (HARMER, 1957, pl. 51, fig. 16) shows the base of one such branch. He also depicts a line down the dorsal side - this is one of two such lines that can be seen when viewed in transparency, each corresponding to the sides of the dorsal carina. HARMER's illustration lacks one avicularium and the dorsal spine (which latter can easily be broken).

Petalostegus vexillum sp. nov.

Pls 3, H-K ; 4, A ; 8, B,C

MATERIAL EXAMINED - **New Caledonia**. — BIOCAL : stn DW 46, 570 m.

SMIB 4 : stn DW 58, 560 m.

DESCRIPTION. — Colony to 27 mm high, the pattern of branching more or less as in the other bushy species. Autozooids 0.29-1.05 mm total length, the cauda ranging from 0.075-0.73 mm in length and the dilatation 0.27-0.37 x 0.19-0.30 mm. Costal shield often quite convex, the mid-proximal costa generally a little larger than the rest, with 4-5 small lacunae between adjacent costae except for the suboral pair which has only a thin suture line. Geniculation almost adjacent to the middle part of the costal shield, just distal to the base of the lateral costa on that side. Orifice about 0.085 mm wide and 0.042-0.064 mm high, tending to be transversely narrower than in the other species. Avicularia always paired, somewhat variable in shape, i.e., squat or projecting and facing obliquely laterally or distolaterally, the palate partly visible from frontal view. Branches terminate in regular-sized autozooids which produce a middistal kenozooidal spine up to 1.30 mm long, with often a second such spine from the geniculation ; sometimes a branch may terminate in a very small autozooid, with the complete complement of 5 costal spines, that also produces a middistal kenozooidal spine. Fertile segment not especially large, borne on the geniculation of a subterminal autozooid by a very short cauda ; the ovicell 0.41 mm long including the spine-like prolongations, 0.26 mm wide, and 0.40 mm deep, the body of the ovicell being not much larger than the maternal zooid which is slightly wider (0.24 mm) than long (0.19 mm), with an extremely short (0.043 mm) cauda so that the fertile segment is closely adjacent to the autozooid that bears it ; maternal zooid with 5 costae in the shield, the smallest one adjacent to the cauda, the suboral pair largest, each with a spinous prolongation directed first forward, then outwards away from, the other ; geniculation proximal, lacking a foramen ; ovicell with an anterior apical prolongation, sometimes expanded distally, with a median suture along its length ; the dorsal prolongation shorter, more spine-like, with a foramen in front of it ; only one avicularium present, the one on the caudal side (adjacent to the parent autozooid) suppressed, with only a foramen present.

TYPES. — *Holotype* : colony from BIOCAL Stn DW 46, 22°53.05′ S, 167°17.08′ E, 570 m, northern Norfolk Ridge, MNHN-Bry 18954.
Paratypes : MNHN-Bry 16635, 16641 and 18952, from same locality as holotype.

DISTRIBUTION. — Northern Norfolk Ridge, 560-570 m.

REMARKS. — *Petalostegus vexillum* autozooids are very similar to those of *P. bicornis* but there are subtle differences - in *P. vexillum* the avicularia face a little to the front instead of to the rear and the orifice tends to be transversely narrower than in *P. bicornis*. The outstanding features of the distinctive fertile segment are the extremely short cauda and suppression of one avicularium.

The species name is a neuter Latin noun used in apposition - it means flag or banner and alludes to the flag-like expansion of the anterior prolongation of the ovicell.

Petalostegus spinosus Powell, 1967

Pl. 4, B-G

Petalostegus spinosus Powell, 1967 : 218, fig. 2 ; pl. 2, a-f.

MATERIAL EXAMINED. — **New Caledonia.** BIOCAL : stn DW 66, 515 m.
SMIB 4 : stn DW 39, 560 m.

DESCRIPTION. — Colony to 27 mm high, the pattern of branching more or less as in the other bushy species, but with a definite main axis. Autozooids 0.47-1.15 mm total length, the cauda ranging from 0.15-0.79 mm in length and the dilatation 0.24-0.43 x 0.20-0.30 mm. Costal shield somewhat inflated, the lateral costa nearest the geniculation generally slightly larger than the rest, with 4-5 lacunae between costae and 2-3 between the suboral pair. Geniculation adjacent to the base of a lateral costa or just distal to it, spur-like. Orifice D-shaped, generally around 0.085 mm wide and 0.050 mm high. Avicularia always paired, somewhat variable in orientation but generally rather elongate and angled across the top of the orifice toward each other, rounded behind, with upturned rostral tips, the palate facing frontally. Branches terminate in regular-sized or rather small (but with a complete costal shield, orifice, and avicularia) autozooids that produce a kenozooidal spine (up to 1.50 mm long) middistally and often also on the geniculation. Fertile segment borne on the geniculation of a penultimate or subpenultimate autozooid by a relatively short cauda ; the body of the ovicell not much longer than the maternal zooid but attaining 0.49 mm depending on the length of the dorsal prolongation, about 0.30 mm wide and up to 0.43 mm deep (depending on the angle of the dorsal prolongation) ; maternal zooid about 0.21 mm long and 0.30 mm wide, the cauda 0.085-0.17 mm long, more or less at right angles to the zooidal axis ; costae 5, the one adjacent to the cauda generally a little smaller than the rest, the oral pair expanded forward as a shelf from which arise a pair of outwardly diverging prolongations ; geniculation proximolateral, lacking a foramen ; ovicell with the apical surface somewhat expanded and triangular owing to a pair of anterior expansions which are upturned frontally, often with denticulations ; a large foramen present in front of the dorsal prolongation ; avicularia paired, facing laterally.

DISTRIBUTION. — Northern New Zealand (near Cape Maria van Diemen), 64-73 m ; northern Norfolk Ridge, 515-560 m.

REMARKS. — This is a very distinctive species, unlikely to be confused with any other. Notable features are the placement and orientation of the autozooidal avicularia, the spurred geniculation of the autozood, and the bizarre excrescences of the fertile segment.

In terms of relationships, *Petalostegus spinosus* is probably closest to *P. vexillum* in the sum of its characters. The maternal zooids of both species are very similar.

Petalostegus tenuis (Maplestone, 1899)

Pl. 4, H

Catenaria tenuis Maplestone, 1899 : 11, pl. 2, fig. 22.

MATERIAL EXAMINED. — Museum of Victoria : Holotype slide 10097.

TYPE MATERIAL. — Unique holotype fragment, Museum of Victoria 10097.

TYPE LOCALITY. — Muddy Creek, near Hamilton, Victoria. Age. - Balcombian (Early Langhian), Lower Miocene.

DESCRIPTION. — Autozooidal fragment 0.51 mm long, the dilatation 0.26 mm long and 0.18 mm wide. Costal shield convex, comprising five petaloid costae, these more or less contiguous where they join, with only a thin suture line and small slit-like gap between the suboral pair and two such slits between the adjacent costae. Orifice high-arched, 0.086 mm wide and 0.067 mm high. Avicularia paired, somewhat columnar, the palate facing more or less frontodistally. Budding sites for other zooids indicated by the geniculate process at the level of the proximal half of the dilatation and a middistal site.

REMARKS. — *Petalostegus tenuis*, known from a single zooid, is the earliest known member of its genus and contemporaneous with the earliest known species of the only other petalostegid genus, *Chelidozoum* (see later).

MAPLESTONE (1899) noted its similarity to *Catenaria bicornis* (the type species of *Petalostegus*) but interpreted the " raised oval area " (the costal shield) as " quite different ". In his illustration MAPLESTONE (1899, pl. 2, fig. 22) misinterpreted the arrangement of the costal spines, of which there are the normal complement of five, but there are several other differences anyway - in *P. tenuis* the gaps between the costae are fewer and so narrow as to be scarcely evident, the geniculate budding site is more proximal on the dilatation, and the avicularia are larger with a more distal orientation.

Genus ***CHELIDOZOUM*** Stach, 1935

DIAGNOSIS. — Main axes of colony composed only of claviform kenozooids, rarely of autozooids ; autozooids mostly only in subterminal positions within branches. Autozooids with a small to moderate costal field of two to five spines, the gymnocyst proportionately extensive ; zooidal dilatation bent forward, the dorsal surface very convex, with some flattening of the anterior half. Orifice sinusoid. Avicularia present or absent or the distolateral corners replaced by pointed projections ; a short claviform avicularium may be produced from claviform kenozooids with opesiae. Fertile zooid with three costal spines (where known), the ovicell large, typically with median suture and distal foramen. Rhizoids issue from axial zooids of primary and/or secondary branches.

RANGE. — Langhian (Lower Miocene) to Recent.

TYPE SPECIES. — *Claviporella vespertilio* MacGillivray, 1895.

Chelidozoum vespertilio (MacGillivray, 1895)

Fig. 3, a, b; Pl. 5, A

Claviporella vespertilio MacGillivray, 1895 : 20, pl. 2, fig. 22.
Chelidozoum vespertilio - STACH, 1935a : 44, figs 4, 5. — BASSLER, 1953 : G224, fig. 168.4.

TYPE MATERIAL. — Holotype, Museum of Victoria, Melbourne, slide P27518.

TYPE LOCALITY. — Muddy Creek, near Hamilton, southwest Victoria, Australia (Lower Miocene).

MATERIAL EXAMINED. — Museum of Victoria : Holotype slide P27518.

DESCRIPTION OF HOLOTYPE. — Autozooid more or less triangular in frontal view, tapering proximally to a short, narrow caudal portion, the dorsal surface bent foward anteriorly more or less at right angles with respect to the caudal axis, with distolateral backwardly directed wing-like expansions tapering to a point, the dorsal surface behind the orifice with some flattening, with a small abutment surface and communication pore for attachment of another segment; median longitudinal length of zooid 0.406 mm, width at distolateral corners 0.449 mm, the depth of the zooid 0.220 mm. Costal shield of moderate size, with 3 broad costae of which the midproximal one is largest. Orifice with a broad rounded sinus delimited by a pair of condyles. Avicularia absent.

DISTRIBUTION. — Lower Miocene, Victoria, Australia.

REMARKS. — MACGILLIVRAY (1895) doubtfully attributed this species (based on a pair of zooids) to *Claviporella*, a catenicellid genus, with the comment, "it may not be a member of the Catenicellidae at all". STACH (1935) with more material available for examination, concluded that it represented a new genus of Savignyellidae, a reasonable conclusion at the time. He did not detect the costal shield (which is barely visible by transmitted light in the holotype zooid) but misleadingly illustrated longitudinal striae and mentioned sparse punctae, neither of which are present in the holotype. The holotype also lacks avicularia, which STACH (1935) mentions in his specimens. He does mention one helpful character however - the presence of two anterodorsal pores, which are found in Recent species descri-

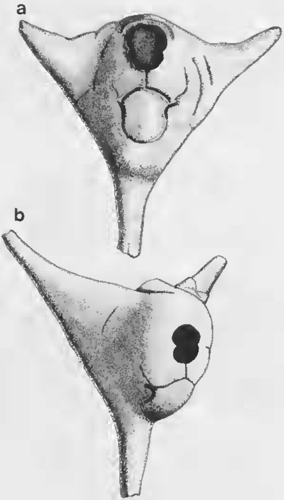


FIG. 3. — a, b. Frontal and partly lateral views of the holotype zooid of *Chelidozoum vespertilio* (MacGillivray). Drawn from SEM photos of the uncoated specimen.

bed here, indicating the presence of kenozooidal spines.

On the basis of the material available to us *Chelidozoum* is clearly a genus of Petalostegidae, as evidenced by the form of the colony, the costal shield, and the characteristic fertile segments. The chief differences from *Petalostegus* are the " bent-forward " shape of the autozooid and the kenozooidal axes in most of the species of *Chelidozoum*.

Chelidozoum quinarium sp. nov.

Pl. 5, B-E

MATERIAL EXAMINED. — **New Caledonia**. BIOCAL : stn DW 08, 435 m. — Stn DW 46, 570 m. — Stn DW 66, 515 m.

DESCRIPTION. — Colony erect, branching, delicate, to 22 mm high, anchored by a basal stem of multiple chitinous rhizoids. Main axes of claviform kenozooids, with long caudae, each of which produces 2 daughter kenozooids. Secondary branches comprise 2-3 series of kenozooidal bifurcations of which the most distal kenozooids produce 2 autozooids ; each of these autozooids produces another autozooid and a spine and the autozooid from this bifurcation produces 2 spines - there are never more than 2 consecutive series of autozooids. Autozooidal dilatation of a peculiar shape - in lateral view it has a more or less triangular profile, with the dorsal surface defining a right angle ; the frontal surface is also more or less triangular in profile and inclined forward away from the secondary branch axis ; frontal length of dilatation 0.33-0.41 mm, the width 0.28-0.34 mm, the depth 0.38-0.43 mm. Orifice wider than long, with conspicuous condyles separating the broad rounded poster from the anter. Frontal shield with a field of 5 flattened costal spines, the median proximal one relatively large, the 2 lateral ones very small, with 2 small lacunae on each side between the spine bases. Avicularia paired, non-projecting, at the distolateral corners of the orifice, with complete cross-bar, the rostrum shortly acute, directed toward the orifice. Posterior half of dorsal surface narrowed like a keel ; anterior half of dorsal surface flattened, subquadrangular, with a pair of foramina, the larger of which, at the top of the keel, is the attachment for the caudal part of an autozooid, the other, smaller, for a spine, or both foramina are small when 2 spines occur. Ovicell not known. Rhizoids issue singly from a dorsal pore in kenozooids.

TYPES. — *Holotype* : a colony from BIOCAL Stn DW 08, 435 m, MNHN-Bry 18958.

Paratypes : colonies from BIOCAL Stn DW 46, 570 m, MNHN-Bry 18951 and Stn DW 66, 515 m, MNHN-Bry 18943.

DISTRIBUTION. — Northern Norfolk Ridge, 435-570 m.

REMARKS. — *Chelidozoum quinarium* is distinguished by the shape of the autozooids and the branching pattern in which autozooids are restricted to the distal ends of otherwise kenozooidal branches. Also, the costal shield has five spines, reflected in the species name (Latin *quinarium*, consisting of five).

Chelidozoum ternarium sp. nov.

Pl. 6, A-J

MATERIAL EXAMINED. — **New Caledonia**. BIOCAL : stn DW 36, 650 m. — Stn DW 44, 440 m. — Stn DW 46, 570 m.
MUSORSTOM 4 : stn DW 222, 410-440 m.

DESCRIPTION. — Colony erect, branching, delicate, to 26 mm high, anchored by a stem of rhizoids. Branching monopodial, with a main axis of claviform kenozooids ; each of these produces 2 daughter zooids, the one contributing to the axis, the other beginning a secondary branch of kenozooids, each of which produces a further kenozooid contributing to the branch and an autozooid. All autozooids are produced on the same side of a secondary branch (distal) ; all secondary branches are produced alternately to left and right along the main axis ; up to 5 autozooids are produced from each secondary branch of which the terminal kenozooid is spine-like ; autozooids themselves rarely produce another autozooid - most produce a dorsal spine or this is lacking. Kenozooids have a distal depression with a small pore and a majority of the secondary kenozooids produce a small, projecting, avicularium. Autozooidal dilatation somewhat claviform, with the dorsal surface bent forward, though not as abruptly as in *C. quinarium*; length of autozooids (plus cauda) 0.40-0.55 mm, the width (not including avicularial projections) 0.23-0.28 mm. Orifice a little wider than long, with stout condyles dividing the broad rounded poster from the anter. Frontal shield smooth, with a small field of 3 costal spines of which the mid-proximal one is smallest; there are no lacunae. Avicularia paired, more usually single, or lacking, situated dorsolaterally, projecting like ears, the rostrum short, acute, directed distally, cross-bar lacking. Fertile segment arising from an autozooid, 0.60 mm long, the ovicell wider (0.29 mm) than the maternal zooid and very deep-bodied; the combined orifice more or less D-shaped, the ovicell with a median carina which is more pronounced apically, and a dorsal chamber opening in front of a spur. Frontal shield of maternal zooid with a field of 3 costae, the proximal one smallest, the oral pair sometimes projecting frontally at their tips. Rhizoids originating as in *C. qrinarium.*

TYPES. — *Holotype* : a colony from BIOCAL Stn DW 44, 440 m, MNHN-Bry 18957.

Paratypes : colonies from BIOCAL Stn DW 36, 650 m, MNHN-Bry 18945. — Stn DW 44, 440 m, MNHN-Bry 18949. — Stn DW 46, 570 m, MNHN-Bry 18941; and MUSORSTOM 4 Stn DW 222, 410-440 m, MNHN-Bry 18946.

DISTRIBUTION. — Northern Norfolk Ridge, 410-650 m.

REMARKS. — The species is named for the three spines in the costal shield in contrast to the five in *C. quinarium* and the two in *C. binarium* and *C. pararium.*

One feature present in *C. ternarium* is shared by *Petalostegus harmeri*, viz., an avicularium produced by kenozooids. HARMER (1957, pl. 51, fig. 13) shows how such an avicularium may be produced by the terminal opesiulate kenozooid in a secondary branch.

Chelidozoum binarium sp. nov.

Pl. 7, A-E

MATERIAL EXAMINED. — **New Caledonia**. SMIB 4 : stn DW 50, 295 m.

DESCRIPTION. — Colony erect, branching, delicate. Autozooids tiny, the length and height of the dilatation the same (0.23-0.28 mm), the width 0.16-0.18 mm, the dorsal surface abruptly bent forward about half-way along, the anterior dorsal surface somewhat convex. Frontal shield smooth, the costal field markedly reduced to a pair of costae that define the V-shaped proximal rim of the orifice. Distolateral corners of the autozooid produced on one or both sides into a long, spine-like avicularium. Ovicell not known.

TYPES. — *Holotype* : slide of colony fragments (autozooids) from SMIB 4 Stn DW 50, 295 m, MNHN-Bry 18948.

DISTRIBUTION. — Northern Norfolk Ridge, 295 m.

REMARKS. — This species was initially confused with *C. ternarium*, although smaller, and inadvertently dissociated in preparation for SEM examination so details of branching are not known. Characteristic features of *C. binarium* include its very small zooids and the long narrow avicularian processes.

The species name *binarium* alludes to the single pair of costae.

Chelidozoum pararium sp. nov.

Pl. 7, F-I

MATERIAL EXAMINED. — **Australia**. Museum of Victoria : stn Slope 32, off Point Hicks, Victoria, 1000 m.

DESCRIPTION. — Colony erect, branching, delicate, to 28 mm high, anchored by numerous rhizoids. Branching monopodial, with a main axis of autozoods, each of which produces 2 daughter zooids, the one contributing to the main axis, the other beginning a secondary branch. Axial autozooids longest, with caudae up to 1.42 mm long. Autozooidal dilatation about 0.41 mm long, 0.23 mm wide, and 0.24 mm deep, somewhat claviform to subtriangular in frontal view, the dorsal surface bent forward at almost right angles to the branch axis. Orifice subcircular, with a broad rounded proximal rim. Frontal shield smooth, with the costal field reduced to a suboral pair. Avicularia single, middorsal, or paired, with the second avicularium substituting for a branch locus ; sessile, no cross-bar. Ovicell unknown.

TYPES. — *Holatype :* colony from Museum of Victoria, Stn Slope 32, 38°21.9'S, 149°20'E, 1000 m, south of Point Hicks, Victoria, slide no. F52880.

Paratype : from same locality, NZOI, P-997.

DISTRIBUTION. — Off Victoria, 1000 m.

REMARKS. — *Chelidozoum pararium* is exceptional among the species of *Chelidozoum* seen so far in that the primary axis is composed of autozooids not kenozooids.

Conceptually, *Chelidozoum pararium* and *C. binarium* are interesting endpoints in a seeming trend in petalostegids from forms with five large costae, through *C. quinarium* where two of the five costae are reduced in size, and *C. ternarium* with only three costae. The species name is a Latin adjective meaning pertaining to two, alluding to the suboral pair of costae.

This evident trend in the reduction of the numbers of costae in petalostegids is mirrored in some catenicellid lineages where the costal field is greatly reduced to become merely components of the proximal orificial rim (see BANTA & WASS, 1979).

SYSTEMATIC AFFINITIES

The genus *Petalostegus*, until recently included in the families Bicellariellidae and Alysidiidae (see GORDON, 1984), has until now been considered an " anascan " genus. However, it is clear that it is most closely related to *Chelidozoum* which, at least from its putative association with the Savignyellidae, has rightly been considered to be in the Ascophorina.

Recently, GORDON (1989a) included the Savignyellidae in the superfamily Catenicelloidea because of the discovery of a vestigial costal field (a suboral pair of spines) in *Vasignyella otophora* (Kirkpatrick). As presently constituted, the Catenicelloidea include the Catenicellidae, Ditaxiporinidae, Eurystomellidae, and possibly Tremoschizodinidae (GORDON, 1989a, b). The superfamily comprises families among whose species are some which have a well-developed spinocyst (costal field) or at least a vestigial spinocyst (a suboral pair of costae defining the proximal rim of the orifice) with concomitant increase in the area of gymnocyst. The Petalostegidae are here considered to be allied to this group of families.

In the table below are listed the definite families of the Catenicelloidea and some of the genera exhibiting the range of spinocyst development in each family.

Family	Earliest known occurrence	Well-developed spinocyst	Reduced spinocyst	Vestigial spinocyst	No spinocyst
Catenicellidae	Thanetian	*Costaticella*	*Pterocella*	*Cribricellina* (part)	*Cornuticella*
Ditaxiporinidae	Ypresian	—	—	*Caberoides* (part)	*Ditaxiporina* (part)
Savignyellidae	Ypresian	—	—	*Vasignyella*	*Savignyella*
Petalostegidae	Langhian		*Petalostegus*	*Chelidozoum* (part)	—
Eurystomellidae	Priabonian	—	—	*Eurystomella* (part)	*Selenariopsis*

The Catenicelloidea are a branch of the fundamentally spinocystal infraorder Cribriomorpha, along with the Bifaxarioidea and Cribrilinoidea (GORDON, 1989b). Conceptually, the Catenicellidae are derivable from the Cribrilinidae. The Ditaxiporinidae, in turn, are derivable from the Catenicellidae and, indeed, may not be separable from the Catenicellidae *sensu stricta* at more than subfamily level - from published illustrations and preliminary examination of the genera *Ditaxipora*, *Plagiopora*, *Ditaxiporina*, and *Caberoides*, the range of frontal-shield morphologies seems to be of the same order as in the Catenicellinae, and the Ditaxiporinidae Cheetham, 1963 may be a junior synonym of the catenicellid subfamily Ditaxiporinae Stach, 1935b, characterised by biserial multizooidal segments. The Savignyellidae seem derivable from the Ditaxiporinidae (or Ditaxiporinae) - zooids of *Vasignyella*, for example, with paired avicularia, seem very similar to the single zooids (perhaps the first members of multizooidal internodes) of *Ditaxiporina septentrionalis* (WATERS, 1891).

The relationships of the remaining two families in the table seem less clear cut and it is likely that the earliest-known occurrences do not reflect the true range in time. The Eurystomellidae comprise the encrusting genus *Eurystomella*, one of whose three species has vestigial costae (GORDON, 1989b) and *Selenariopsis*, a rooted discoidal deep-sea genus of a single species, with no trace of costae (COOK & CHIMONIDES, 1981). *Eurystomella*, in the form of its zooids and dimorphic orifices (wider in brooding zooids), is very reminiscent of some species of *Orthoscuticella* (Catenicellidae) and may be derivable from that family through adaptation to an encrusting mode of life.

The affinities of the Petalostegidae are the most obscure of the catenicelloidean families but the trend in reduction of the costal field within a single genus is instructive. *Chelidozoum* thus seems more derived than *Petalostegus*. The enlarged ovicells in *Petalostegus* species are reminiscent of those which occur among the Catenicellidae but the form of the autozooid and the diversification of kenozooidal morphology and function are distinctive features. Very probably there are undiscovered petalostegids from the early Tertiary with morphologies more indicative of systematic affinities than the later species, but probably the Catenicellidae is the most closely related family.

In this regard, the trends summarised in the above table would indicate some morphological possibilities not occurring in known fossil and Recent species. Thus it is theoretically possible that the earliest members of some of the families had larger costal fields, and/or multiple costae; on the other hand, it is possible that a petalostegid may be found which lacks even the vestigial suboral pair of costae.

BIOGEOGRAPHY AND ECOLOGY

The Petalostegidae are entirely southern hemispheric in distribution (although only just), ranging from 0°29'S in Indonesia (*Petalostegus harmeri*) to 45°27'S in New Zealand (*P. trimorphus*). The family is known chiefly from the western Pacific Ocean but ranges east to the Society Islands and is also known from eastern South Africa (*P. [?]bicornis*). The northern Norfolk Ridge contains the greatest concentration of species, with as many as five species occurring at a single station!

The family ranges in depth from 64 m (*Petalostegus spinosus* in northern New Zealand) to 3548 m (*P. bicornis* near Tahiti), with the genus *Chelidozoum* occurring within the ranges for *Petalostegus*. Thus *Chelidozoum* is known only from 295 m (*C. binarium*) to 1000 m (*C. pararium*) and over a small latitudinal range from 20°34'S (*C. quinarium* near New Caledonia) to 38°22'S (*C. pararium* off Victoria).

The family ranges in time, with both genera known from a limited number of early Langhian (Lower Miocene) localities near Hamilton, Victoria, Australia. However, no fossils have been found earlier or later than this age although they undoubtedly must occur. The occurrence of four new Recent species of the previously monotypic fossil genus *Chelidozoum* is of particular interest, along with the fact that both it and *Petalostegus* occur together in Miocene and Recent faunal assemblages.

New Zealand and New Caledonia, linked by the Norfolk Ridge, a sliver of continental margin (EADE, 1988), have been separated by open ocean from the rest of Gondwanaland since the Santonian (Late Cretaceous), about 85 mya (STEVENS, 1985). At this time the earliest-known unbonulomorph species occurs, postdating the earliest-known hippothoomorph (Coniacian) and cribriomorphs (Cenomanian) in Europe (VOIGT, 1991). By the Ypresian (early Eocene) the Tasman Sea probably reached its present width

(EADE, 1988). The earliest catenicellid (subfamily Catenicellinae) is known from the Thanetian (Palaeocene), from a DSDP drilling site in the North Atlantic (CHEETHAM & HAKANSSON, 1972); it is likely that the Petalostegidae are derived from this subfamily, which was present in Victoria by at least the Chattian (Late Oligocene) (LAGAAIJ & COOK, 1973). The catenicellid subfamily Ditaxiporinae is also known from Victoria at this time (BROWN, 1958) - the significance of this is that the ditaxiporine genus *Plagiopora*, previously known only from the Miocene of Victoria, is, like *Chelidozoum*, found alive on the Norfolk Ridge (GORDON, 1989c). So the problem is one of explaining how these two genera, from different families, came to be present on either side of the Tasman Sea at a time when any shallow-water links between south-eastern Australia and the New Caledonia-New Zealand axis are assumed to have been severed (STEVENS, 1985). One possibility is that these genera have a longer occurrence in time than is presently appreciated from their limited distribution as fossils, perhaps as early as late Eocene, with a southwards differentiation into Victoria and New Caledonia from northern progenitors before the Miocene when the nortbern Tasman Sea area was shallower and narrower. Inasmuch as Recent *Chelidozoum* occurs to 1000 m and *Plagiopora* to 831 m, traversing deeper areas of seafloor between topographic highs may not have been an insurmountable problem.

Ecologically, the rooted colonies of petalostegids are able to occur on a range of substrata ranging from rock to foraminiferal mud. The exact kind of substratum is not known for most of the species, but *Petalostegus bicornis* and *P. trimorphus* are known to anchor to clusters of foram grains. The dendroid colonies of both *Petalostegus* and *Chelidozoum* are settled by epizoites. These include unidentifiable juvenile colonies of tubuliporine bryozoans and especially foraminiferans.

Of particular interest is evidence of mollusc predation. Boreholes were found in ovicells of *Petalostegus bicornis* and *P. vexillum* from BIOCAL Stn DW 46 and *P. bicornis* from BIOCAL Stn CP 61 (Pl. 8, A-C). Similar boreholes were found in both ovicells and autozooids of *Domosclerus* sp. from BIOGEOCAL Stn CP 232. The *Petalostegus* boreholes are about 0.075 mm diameter - those in *Domosclerus* are 0.17-0.22 mm diameter, indicating two species of predator or different size ranges of the same species. On one branch of *Domosclerus* sp. five consecutive zooids/ovicells have boreholes, indicating the predator worked its way systematically along at least part of the branch, and, overall, slightly more autozooids were bored than ovicells. TAYLOR (1982) is the only author to have reported on putative boreholes in bryozoans. He recorded these in four species of late Cretaceous melicerititids and Recent *Celleporina rota* (MACGILLIVRAY) from Victoria, Australia. The boreholes were circular to oval in shape, ranging from 0.04-0.09 mm in diameter, similar to those found in Norfolk Ridge bryozoans.

TAYLOR (1982) noted that autozooids scored more borings than the avicularia-like heterozooids in *Meliceritites*; and that the borings in *Celleporina rota* occurred in the frontal shields of autozooids. Polypides would certainly afford food of reasonable caloric value, however the yolky embryos contained in ovicells would be far more energetically rewarding to a predator. It is possible that a predator is unable to discern the contents of bryozoan chambers but it is also true that in cheilostomes with ovicells, large yolky eggs are found in maternal-zooidal body cavities prior to their passage into ovicells for brooding as larvae. In the limited sample available, maternal zooids are bored as frequently as autozooids in *Domosclerus*. It seems significant that, in *Petalostegus*, in which ovicells are not that abundant, only they are bored.

The identity of the predators is not known. TAYLOR (1982), on the basis of what is known about molluscan boreholes, suggested nudibranchs or tiny muricids, perhaps juveniles, as the predators of melicerititids. Other possibilities are small naticids, octopods, and even nematodes (see KABAT, 1990 : 157).

ACKNOWLEDGEMENTS

We want to extend our special thanks to the following people : Mary SPENCER-JONES (The Natural History Museum, London) and Rosemary SWART (Museum of Victoria, Melbourne), for the loans of specimens ; Pat Cook (Museum of Victoria) and Phil Bock (Royal Melbourne Institute of Technology) for the opportunity to describe their new species of *Chelidozoum* from Victoria ; Karl Majorhazi for his skilful drafting of the figures ; and Rose-Marie Thompson for typing the manuscript.

REFERENCES

Banta, W.C. & Wass, R.E., 1979. — Catenicellid cheilostome Bryozoa 1. Frontal walls. *Austr. J. Zool.*, suppl. ser., no. 68 : 1-70.

Bassler, R.S., 1953. — Bryozoa. Part G. *In* : R.C. Moore, *Treatise on Invertebrate Paleontology*, Geological Society of America and University of Kansas Press, New York : i-xiii, 1-253.

Brown, D.A., 1958. — Fossil cheilostomatous Polyzoa from south-west Victoria. *Mem. Geol. Surv. Vict.* , **20** : 1-90.

Busk, G., 1852. — An account of the Polyzoa, and sertularian zoophytes, collected in the voyage of the Rattlesnake, on the coasts of Australia and the Louisiade Archipelago, &c. *In* : J. MacGillivray, *Narrative of the voyage of H.M.S. Rattlesnake, commanded by the late Captain Owen Stanley ... 1846-1850 ; including discoveries and surveys in New Guinea, the Louisiade Archipelago, etc., to which is added the account of Mr E.B. Kennedy's expedition for the exploration of the Cape York Peninsula [including Mr W. Carron's narrative]*, W. Boone, London : **1**, 343-402, pl. 1, in Vol. 1 (Appendix N° IV).

Busk, G., 1884. — Report on the Polyzoa collected by H.M.S. *Challenger* during the years 1873-76. Part 1. - The Cheilostomata. *Rep. scient. Res. Voyage Challenger, Zoology*, **10**(30) : i-xxiv, 1-216, pls 1-36.

Canu, F. & Bassler, R.S., 1927. — Classification of the cheilostomatous Bryozoa. *Proc. U.S. natn. Mus.*, 69(14) : 1-42, 1 pl.

Canu, F. & Bassler, R.S., 1929. — Bryozoa of the Philippine region. *Bull. U.S. natn. Mus.*, 100 : i-xi, 1-685, pls 1-94.

Cheetham, A.H., 1963. — The polyzoan genus *Ditaxiporina* Stach. *Ann. Mag. nat. Hist.*, ser. 13, **5** : 485-490.

Cheetham, A.H. & Hakansson, E. 1972. — Preliminary report on Bryozoa (Site 117). *In* : A.S. Laughton, W.A. Berggren, *et al.*, *Init. Rep. Deep Sea Drilling Proj.* **12** : 432-441.

Cook, P.L. & Chimonides, P.J., 1981. — Morphology and systematics of some rooted cheilostome Bryozoa. *J. nat. Hist.*, **15** : 97-134.

Eade, J.V., 1988. — The Norfolk Ridge System and its margins. *In* : A.E.M. Nairn, F.G. Stehli, & S. Uyeda, *The ocean Basins and Margins, vol. 7b, the Pacific Ocean*, Plenum, New York & London : xiv, 1-642 p.

Gordon, D.P., 1984. — The marine fauna of New Zealand : Bryozoa : Gymnolaemata from the Kermadec Ridge. *Mem. N.Z. oceanogr. Inst.*, **91** : 1-198.

Gordon, D.P., 1986. — The marine fauna of New Zealand : Bryozoa : Gymnolaemata (Ctenostomata and Cheilostomata Anasca) from the western South Island continental shelf and slope. *Mem. N.Z. oceanogr. Inst.*, **95** : 1-121.

Gordon, D.P., 1989a. — Intertidal bryozoans from coral reef-flat rubble Sa'aga, Western Samoa. *N.Z. Jl Zool.*, **16** : 447-463.

Gordon, D.P., 1989b. — The marine fauna of New Zealand : Bryozoa : Gymnolaemata (Cheilostomida Ascophorina) from the western South Island continental shelf and slope. *Mem. N.Z. oceanogr. Inst.*, **97** : 1-158.

Gordon, D.P., 1989c. — New and little-known genera of cheilostome Bryozoa from the New Zealand region. *J. nat. Hist.*, **23** : 1319-1339.

Harmer, S.F., 1926. — The Polyzoa of the Siboga Expedition. Part 2. Cheilostomata Anasca. *Siboga-Expeditie*, 28b : i-viii, 18[1]-501, pls 13-34.

Harmer, S.F., 1957. — The Polyzoa of the Siboga Expedition. Part 4. Cheilostomata Ascophora. **II.** *Siboga-Expeditie*, 28d : i-xv, 641-1147, pls 42-74.

Hayward, P.J. & Cook, P.L., 1979. — The South African Museum's *Meiring Naude* cruises. Part 9 Bryozoa. *Ann. S. Afr. Mus.*, **79**(4) : 43-130.

Jelly, E.C., 1889. — *A Synonymic Catalogue of the Recent Marine Bryozoa.* Dulau & Co., London : i-xv, 1-322 p.

Kabat, A.R., 1990. — Predatory ecology of naticid gastropods with a review of shell boring predation. *Malacologia* **32** : 155-193.

Lagaaij, R. & Cook, P.L., 1973. — Some Tertiary to Recent Bryozoa. *In* : A. Hallam, *Atlas of Paleobiogeography*, Elsevier, Amsterdam : 489-498.

Larwood, G.P., 1969. — Frontal calcification and its function in some Cretaceous to Recent cribrimorph and other cheilostome Bryozoa. *Bull. Brit. Mus. (Nat. Hist.), Zool.*, **18**(5) : 171-182.

Levinsen, G.M.R., 1909. — *Morphological and systematic studies on the cheilostomatous Bryozoa*, Nationale Forfatteres Forlag, Copenhagen : i-vii, 1-431, pls 1-24.

MacGillivray, P.H., 1895. — A monograph of the Tertiary Polyzoa of Victoria. *Trans. R. Soc. Vict., n.s.*, **4** : 1-166, pls 1-22.

Maplestone, C.M., 1899. — Further descriptions of the Tertiary Polyzoa of Victoria. - Part 11. *Proc. R. Soc. Vict., n.s.*, **12** : 1-13, pls 1-2.

Powell, N.A., 1967. — Polyzoa (Bryozoa) - Ascophora - from North New Zealand. Discovery Rep., 34 : 199-393, pls 1-17.

STACH, L.W., 1935a. — Victorian Tertiary Catenicellidae (Bryozoa). Part III. *Proc. R. Soc. Vict., n.s.*, **48** : 27-49.

STACH, L.W., 1935b. — The genera of Catenicellidae. *Proc. R. Soc. Vict., n.s.*, **47** : 389-396.

STEVENS, G.R., 1985. — *Lands in Collision - Discovering New Zealand's past geography*, [DSIR Inf. Ser. 161], DSIR, Wellington : 1-129.

TAYLOR, P.D., 1982. — Probable predatory borings in late Cretaceous bryozoans. *Lethaia*, **15** : 67-74.

VOIGT, E., 1991. — Mono- or polyphyletic evolution of cheilostomatous bryozoan divisions? *In* : F.P. BIGEY, *Bryozoaires actuels et fossiles : Bryozoa living and fossil*, [*Mem. Soc. Sci. nat. Ouest Fr. h.s.*] Nantes : 505-522.

WATERS, A.W., 1889. — Supplementary report on the Polyzoa collected by H.M.S. Challenger during the years 1873-1876. *Rep. scient. Res. Voyage "Challenger"*, **31**(79) : 1-141, pls 1-3.

WATERS, A.W., 1891. — North Italian Bryozoa. *Q. Jl geol. Soc. Lond.*, **47** . 1-34, pls 1-4.

PLATE 1

A-F, *Petalostegus bicornis* (Busk): **A**, frontal view of autozooid (× 158) ; **B**, **C**, lateral views of autozooids (× 102 ; × 96) ; **D**, **E**, **F**, frontal, lateral, and distal views of fertile segments - note the distal borehole in D (× 104 ; × 104 , × 106). (A, B, F, BIOGEOCAL Stn CP 214 ; C, D, BIOCAL Stn CP 61 ; E, BIOCAL Stn DW 46.)

G-L, *Petalostegus scopulus* sp. nov.: **G, H,** frontal views of two autozooids, showing variable orientation of avicularia (× 92 ; × 94) ; **I-K**, frontal, lateral, and distal views of fertile segments (× 93 ; × 96 ; × 93) ; **L**, enlargement, tilted, of part of zooid shown in I (× 200). (G-L, BIOCAL Stn DW 66.)

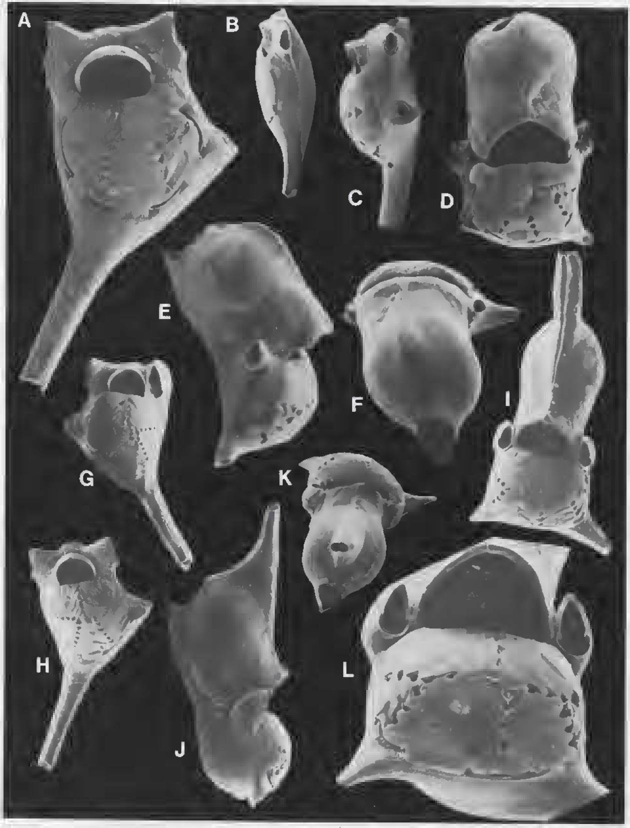

A
B
C
D
E
F
G
H
I
J
K
L

PLATE 2

A-E, *Petalostegus trimorphus* sp. nov. : **A, B**, frontal views of autozooids · note the hole at the top of the cauda where a rhizoid originates (× 183 ; × 182). **C**, terminal autozooid with two spine-like avicularia and a kenozooidal spine (× 67) ; **D, E**, frontal and lateral views of fertile segments - the terminal projection is lacking in D (× 81 ; × 81). (A-C, E, NZOI Stn G675 ; D, NZOI Stn E906.)

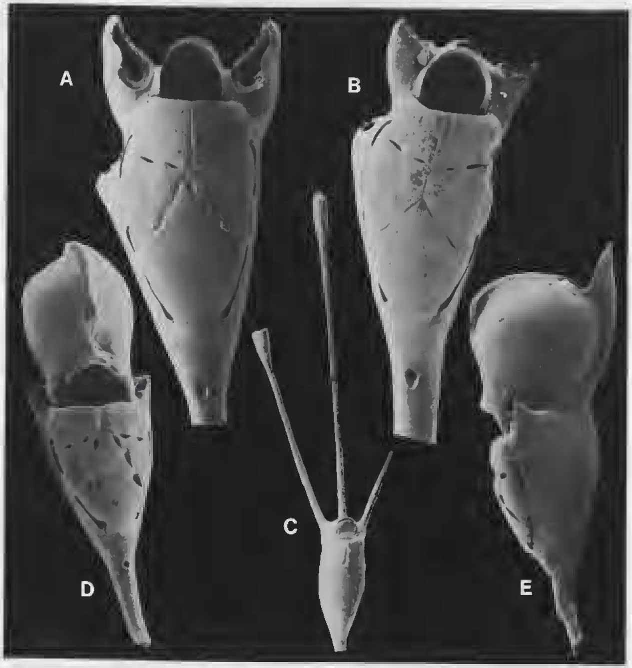

A
B
C
D
E

PLATE 3

A-G, *Petalostegus harmeri* sp. nov. : **A-C**, frontal views of autozooids - C is an axial zooid (× 114 ; × 147 ; × 110) ; **D-G**, frontal, lateral, and distal views of fertile segments - D and E have a vestigial sixth spine base (arrows), and F lacks the distal projection (× 122 ; × 128 ; × 97 ; × 129). (A, F, BIOCAL Stn DW 70 ; B-E, G, BIOCAL Stn DW 66.)

H-K, *Petalostegus vexillum* sp. nov. : **H**, frontal view of autozooid (× 109) ; **I-K**, frontal, lateral, and distal views of fertile segments - note the borehole in K (× 138 ; × 129 ; × 131). (H-K, BIOCAL Stn DW 46.)


A
B
E
D
C
F
G
I
H
J
K

PLATE 4

A, *Petalostegus vexillum* sp. nov. : frontal view of autozooid (× 153). (BIOCAL Stn DW 46.)

B-G, *Petalostegus spinosus* Powell : **B**, frontal view of autozooid (× 160) ; **C-G**, frontal, profile, and distal views of fertile segments - the frontal processes of the ovicell are not fully formed in C (× 143 ; × 83 ; × 93 ; × 160 ; × 141). (B-F, BIOCAL Stn DW 66 ; G, SMIB 4 Stn DW 39.)

H, *Petalostegus tenuis* (Maplestone) : frontal view of dilatation of holotype zooid - SEM of uncoated specimen (× 275). (Museum of Victoria).


A
B
D
C
F
E
G
H

PLATE 5

A, *Chelidozoum vespertilio* (MacGillivray) : distofrontal view of holotype zooid (tilted forward) - SEM of uncoated specimen (× 161). (Museum of Victoria).

B-E, *Chelidozoum quinarium* sp. nov. : **B**, part of colony showing branching (× 67) ; **C-E**, frontal and lateral views of autozooidal dilatations (× 158 ; × 167 ; × 167). (B, BIOCAL Stn DW 08 ; C-E, BIOCAL Stn DW 46).

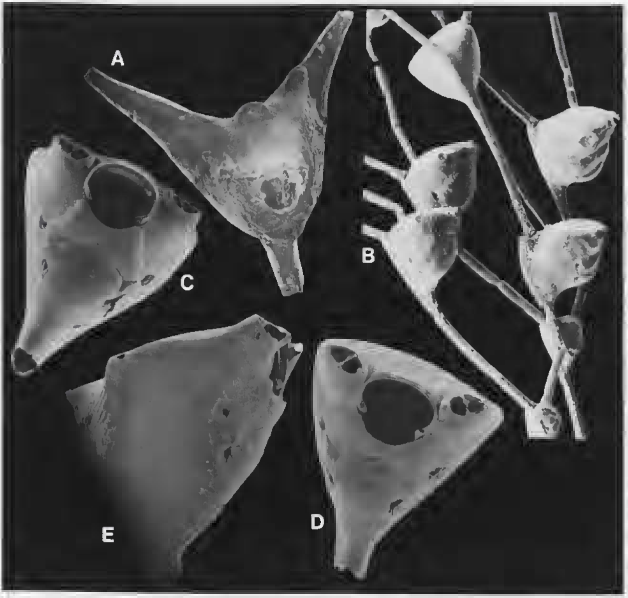

A
B
C
D
E

PLATE 6

A-J, *Chelidozoum ternarium* sp. nov. : **A**, colony, showing branching (× 12) ; **B**, axial kenozooid of a secondary branch with avicularium (× 216) ; **C**, **D**, frontal and lateral views of autozooids (× 234 ; × 106) ; **E**, **F**, two different morphotypes showing variation in length of avicularium (× 111 ; × 106) ; **G**, **H**, frontal, and lateral views of fertile segment (× 148 ; × 151) ; **I**, avicularium (× 911) ; **J**, internal view of orifice and costal field (× 480). (A, BIOCAL Stn DW 46 ; B, E, BIOCAL Stn DW 36 ; C, D, F-J, BIOCAL Stn DW 44.)

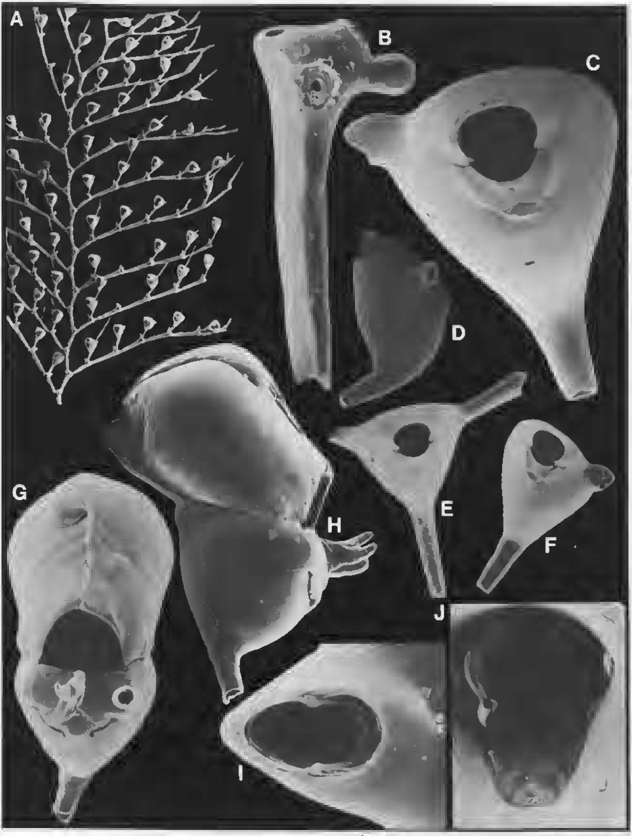

A
B
C
D
E
F
G
H
I
J

Plate 7

A-F, *Chelidozoum binarium* sp. nov. : **A, B,** profile and frontal view of autozooids (× 255 ; × 184) ; **C,** anterodorsal view of autozooid (× 128) ; **D, E,** orifice and vestigial costal field (× 972 ; × 1538). (Smib 4 Stn DW 50.)

F-I, *Chelidozoum pararium* sp. nov. : **F-H,** frontal, lateral, and anterodorsal views of autozooid (× 154 ; × 205 ; × 167) ; **I,** orifice (× 1350). (Museum of Victoria).

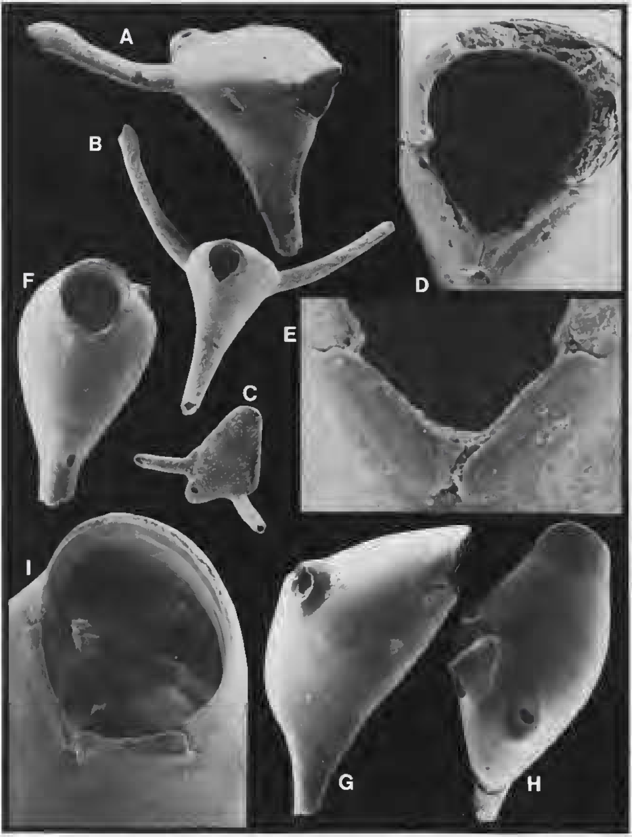
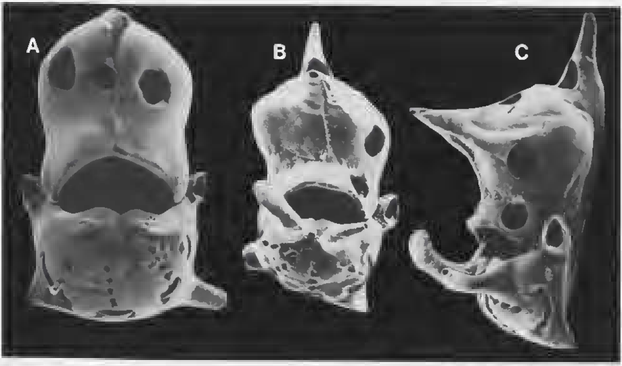

A
B
C
D
E
F
G
H
I

PLATE 8

A, *Petalostegus bicornis* (BUSK) (× 137), and **B, C,** *Petalostegus vexillum* sp. nov. (same fertile segment), showing boreholes of predators (× 120 ; × 137). (A-C, BIOCAL Stn DW 46.)


A
B
C